

Natural regeneration dynamics of three dry deciduous forest species in Chacocente Wildlife Reserve, Nicaragua

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Abstract: A study was conducted to examine the natural regeneration of three dry forest species, *Lysiloma divaricatum* (Jacq.), *Tabebuia ochracea* (Cham.) and *Lonchocarpus minimiflorus* (Donn. Sm.) over a three-year period and to analyze heterogeneity of regeneration in relationship to topographic slope and incidence of light in Chacocente Wildlife Reserve in Nicaragua. Permanent sample plots were established in 2001, and all individuals with height as low as 10 cm and diameter as large as 10 cm were recorded for three consecutive years from 2001 to 2003. The results show that the density of naturally regenerated individuals varied significantly among species, as well as over time. *L. minimiflorus* and *T. ochracea* had higher densities compared with *L. divaricatum*, and the net change in population density was slightly positive for *T. ochracea* only. Regeneration was more abundant in the gentle and steep slopes under partial exposure of the crown to sunlight, thus resulting in aggregated pattern of distribution, especially for *L. minimiflorus* and *T. ochracea*. We concluded that natural regeneration alone is not sufficient to maintain the desired number of stocks of these species, and an immediate restoration measure should be taken to assist the natural regeneration process.

Key words: Central America, mortality, regeneration niche, spatial pattern, dry forest

Introduction

Historical evidences indicate that tropical dry forest in Central America has been extensively converted into other land use types, such as agriculture and/or pasture (Brown and Lugo 1990). The remaining forest patches probably represent less than 2% of the original dry forest along the Pacific coast of Mesoamerica, an area extending from Panama to western Mexico (Sabogal and Valerio 1998). According to Kalacska et al. (2004), the dry forests in many areas of Central America are no more a pristine old-growth forest, but rather a mosaic of secondary forest formations. Nicaragua has 100 000 ha of dry forest located mainly in the Pacific coast (Roldan 2001). The deforestation rate for the period 1990–2000 was estimated about 190 000 hectares per year (Roldan 2001). Therefore, there is a major concern to protect the remaining patches and rehabilitate the disturbed forests.

Natural regeneration is the cheapest approach to rehabilitate a given forest ecosystem if the previous disturbance has left some residuals (e.g. soil seed banks, mother trees, sprout) that can serve as “succession primers” (Teketay 1997). Thus, the first step in any forest rehabilitation endeavor is a site assessment to quantify actual and potential levels of natural regeneration and to determine whether interventions are needed to expedite the natural regeneration process. For restoration by natural regeneration to be effective, adequate knowledge about population dynamics, such as annualized rate of population change, life history of the species, seed- and seedling related recruitment limitations is needed. Equally important is the spatial distribution of the regenerated individuals (Condit et al. 2000), as natural regeneration is often heterogeneous, depending on seed dispersal, viability, dormancy, predation, herbivory, rainfall, topographic, edaphic and light conditions (Kitajima and Fenner 2000; McLaren and McDonald 2003; Enoki and Abe 2004). Topography, through its effect on drainage, moisture and nutrient variation from ridge top to valley bottom, plays an essential role in spatial distribution of recruits (Enoki et al. 1997; Enoki and Abe 2004). The forest canopy structure influences the availability of understory light and the understory environment; thereby influence the understory population (Yirdaw and Luukkanen 2004; Lemenih et al. 2004).

Unlike tropical rain forests that have been extensively studied, the natural regeneration processes (e.g. seed germination, seedling establishment, population change, and spatial patterns) of dry forest species are not yet well documented (Guariguata 1998; Khurana and Singh 2001). Most of the studies on dynamics of

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natural regeneration and spatial distribution of dry forest species in Central America have been carried out in Mexico and Costa Rica (Hubbell 1979; Rico-Gray et al. 1988; Gerhardt 1996). Some studies focused on floristic composition and population dynamics in Nicaragua (Sabogal and Valerio 1998; Gillespie et al. 2000; Castro-Marin et al. 2005; Gonzalez-Rivas et al. 2006), but no account of the spatial heterogeneity of natural regeneration of dry forest species in this country exists.

In this study, we examined the natural regeneration of three dry forest species, *Lysiloma divaricatum* (Jacq.), *Tabebuia ochracea* ssp. *Neochrysantha* (Cham.), and *Lonchocarpus minimiflorus* (Donn. Sm.), over a three-year time and in relationship to topography and light incidence, to examine temporal variation in population density of seedlings, saplings and poles and to analyze heterogeneity of natural regeneration in relation to topography and incidence of light. Topography was quantified by slope steepness and incidence of light by crown exposure of individual recruits to direct sunlight as fully exposed, partially shaded and overshadowed.

Methods

The study area

The study was conducted in dry forest of Chacocente Wildlife Reserve (11°36'–11°30' N and 86°08'–86°15' W) located on the Pacific coast in the department of Carazo. The total area of the reserve is 4 645 ha, of which 2 941 ha is the core dry deciduous forest, 471 ha is gallery forest along the main water course, the Río Escalante, 554 ha is scrubs, 311 ha is annual crop land, 294 ha is grass land and 71 ha is beach (Anonymous 2002). The altitude ranges from sea level to 300 m.a.s.l (Sabogal 1992). The soil in the deciduous forest is Vertic and Ferric Luvisol and Eutric fluvisol in the gallery forest (Sabogal and Valerio 1998). According to Holdridge's system the area is classified as tropical dry forest. The mean annual temperature from 1984 to 2003 is 26.7±0.26°C and the mean total annual precipitation is 1440.52±370.7 mm. The dry period spans over five month, from December to April.

Species description

The species investigated in the present study were *L. divaricatum*, *L. minimiflorus* and *T. ochracea*. The first two species are small to medium-size leguminous trees, which occur in deciduous and evergreen forests of Mexico and Central America. *T. ochracea* (Bignoniaceae) is a medium-sized to large tree widely distributed in deciduous and evergreen forests of Mexico, Central America, Venezuela, Brazil and Ecuador. In Nicaragua, these species are the main sources of wood for rural constructions, firewood and furniture production (Cordero et al. 2004; Steven et al. 2001).

Inventory of natural regeneration

Permanent sample plots were established in 2001 following a systematic design in which 200 plots of 100 m² (20m × 5m) were

laid down continuously along 4 transects. The length of each transect was of 1 km and the distance between two adjacent transects was 800 m. The sample plots covered the variation in environmental gradients, especially topography and incidence of light. All individuals with height as low as 10 cm and with diameter at breast height (dbh) as large as 10 cm were recorded for three consecutive years from 2001 to 2003. Regenerated individuals were classified according to size as follows: Individuals with height from 10 to 100 cm were considered as seedlings, individuals with height above 100 cm and dbh as large as 5 cm were classified as sapling and those with dbh between 5 cm and 10 cm were considered pole. The measurements were carried out during the end of rainy season at all occasions.

For each individual recruit, the degree of crown exposure to direct sunlight was visually determined as overshadowed, partially shaded and fully exposed (Hawthorne 1993). The percent slope of each plot was determined, and a slope class was constructed as follows: flat or nearly flat (0–2%); gentle slope (2–13%) and steep slope (>13%) following approved practice (FAO 1977; Faniran and Areola 1978; Bosworth and Foster 1982). The number of plots belonging to flat, gentle and steep slope classes was 32, 85, and 83, respectively.

Data analysis

The total number of individuals was computed for each species, size class and year (2001, 2002 and 2003). The number of individuals per species was also determined in relation to the degree of crown exposure to direct sunlight and slope classes. For each species, annualized rate of population change (r) was computed using a standard logarithmic growth model (Condit et al. 1996) as:

$$r = \frac{\ln N_{03} - \ln N_{01}}{t} \quad (1)$$

Where, N_{03} and N_{01} are the population sizes in 2003 and 2001, \ln is the natural logarithm, and t is the time interval between two assessments. Annualized rate of population change was also calculated for each size class, degree of crown exposure to direct sunlight and slope classes. We assumed that mortality would vary among seedlings that were fully exposed and overshadowed due to dry season drought. Mortality was also assumed to vary with slope of the terrain mainly through its effect on drainage, moisture and nutrient availability.

Chi-square analysis was performed to examine temporal variation in density of seedlings and saplings. The density of poles was not included in the analysis because it was very low and only one species had individuals in pole size. The chi-square analysis was also employed to examine whether the total density of naturally regenerated individuals vary between the different slope classes and crown exposure to direct sunlight. For this particular analysis, the total density, a sum of the density of seedlings and saplings, was first computed for each census year and then the mean value of the three census years was used. As the number of plots and the corresponding area belonging to the different slope class was different, the estimated density was

weighted by the area of each slope class. *L. divaricatum* was not included in the analysis due to its low density that violates the assumption for Chi-square analysis. To further account the spatial pattern of regeneration, the Standardized Morisita's Index (I_p) was calculated for each species using the mean density across the census year. There are a number of spatial indices, but I_p is independent of population density and sample size (Krebs 1999). I_p ranges from -1.0 to +1.0 with 95% confidence limits at ± 0.5 . The distribution of a population was considered random, clumped or uniform if $I_p = 0$, $I_p > 0$ or $I_p < 0$, respectively. It was calculated as follows: First the Morisita's index was computed as:

$$I_d = n (\sum x^2 - \sum x) / [(\sum x)^2 - \sum x] \quad (2)$$

where, n is the sample size, $\sum x$ and $\sum x^2$ are the sum of the quadrat counts, and the sum of the quadrat counts square, respectively. Then two critical values for the Morisita's index were calculated using the following equations:

Uniform index; $M_u = (X^2_{0.975} - n + \sum x_i) / (\sum x_i - 1)$

Clumped index; $M_c = (X^2_{0.025} - n + \sum x_i) / (\sum x_i - 1)$

Where $X^2_{0.975}$ and $X^2_{0.025}$ are the values of chi-squared with $(n-1)$ degrees of freedom that has 97.5% and 2.5% of the area to the right, respectively; x_i = given a set of counts of organisms in a set of quadrats and n = number of quadrats

Finally, the standardized Morisita's index was calculated using

the relevant formula out of the following four:

1. $I_p = 0.5 + 0.5 (I_d - M_c) / (n - M_c)$; when $I_d \geq M_c > 1.0$
2. $I_p = 0.5 (I_d - 1) / (M_u - 1)$; when $M_c \geq I_d > 1.0$
3. $I_p = -0.5 (I_d - 1) / (M_u - 1)$; when $1.0 > I_d > M_u$
4. $I_p = -0.5 + 0.5 (I_d - M_u) / M_u$; when $1.0 > M_u > I_d$

Results

Temporal variation in density

The density of seedlings, saplings and poles of the studied species across the census years varied among species (Fig. 1). For *L. minimiflorus*, the total density ($X^2_{(0.05, 2)} = 9.87$, $p = 0.007$) and the density of seedlings varied significantly over time ($X^2_{(0.05, 2)} = 33.86$, $p < 0.0001$) while no significant difference was observed in density of saplings across the census period. For *T. ochracea*, no significant difference was found in total density as well as in the density of each size class over time. Among species, *L. minimiflorus* and *T. ochracea* had the highest densities compared with *L. divaricatum*. *T. ochracea* was the only species represented by poles, albeit low in density.

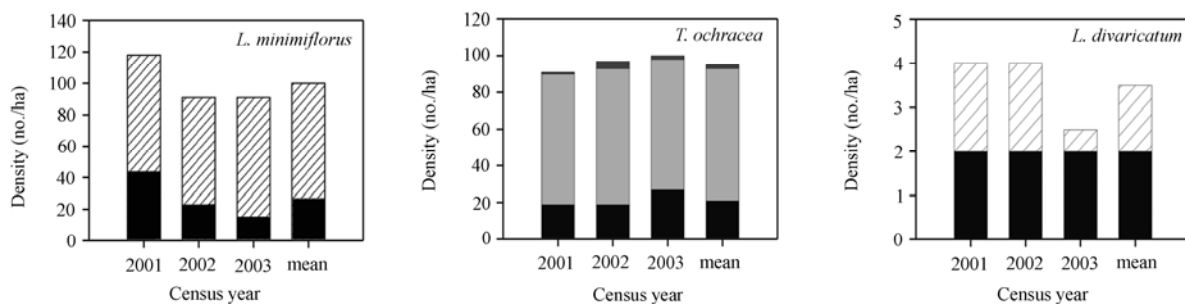


Fig. 1. Population density of seedlings, saplings and poles of the studied species over a three-year period and mean densities across the census years. For *L. minimiflorus* and *L. divaricatum*, shaded black bars represent seedlings while striped bars are for saplings. For *T. ochracea* shaded black, light grey and heavy grey bars represent seedling, sapling and pole densities, respectively.

The annualized rate of population change varied considerably for each size class of the studied species (Table 1). The density of *L. minimiflorus* seedlings decreased by 54%, while the density of saplings increased by 2%. For *T. ochracea*, the density of seedlings, saplings and poles increased by 18%, 0.4% and 46%, respectively. For *L. divaricatum*, there was a 69% loss of saplings compared with a slight increase in the density of seedlings (11%). As a whole, the net change in total population density was slightly positive for *T. ochracea* (5%) only.

Density in relation to topographic slope

The mean population density (averaged over the three census years) of seedlings and saplings of the studied species differed significantly in relation to slope of the terrain ($X^2_{(0.05, 2)} = 53.654$, $p < 0.0001$ for *L. minimiflorus*, $X^2_{(0.05, 2)} = 54.584$, $p < 0.0001$ for *T. ochracea*). For both species, the mean total density (seedlings plus saplings) was much lower in the flat than in either the gentle

or steep slope (Fig. 2). For *L. minimiflorus*, the mean total density was considerably higher in the gentle slope than the steep slope. There was an increasing tendency in mean total density of *T. ochracea* with increasing slope of the terrain. The mean density of *L. divaricatum* was equally low in all slope classes.

Table 1. Annual rate of change in density of seedlings, saplings, pole and total density of *Lonchocarpus minimiflorus*, *Tabebuia ochracea* and *Lysiloma divaricatum* over a two-year period in Chacocente dry forest

Size class	Annualized rate of population change (r)		
	<i>L. minimiflorus</i>	<i>T. ochracea</i>	<i>L. divaricatum</i>
Seedling	-0.544	0.176	0.112
Sapling	0.017	0.004	-0.693
Pole	----	0.458	----
Total	-0.129	0.052	-0.144

--- data not available

The annualized rate of population change for *L. minimiflorus* showed a slight increase in the flat (4%), but reduced by 12%

and 17% in the gentle and steep slopes, respectively over the census years (Table 2). For *T. ochracea*, there was an increase in population by 17%, 7% and 3% in flat, gentle and steep slopes, respectively. The population of *L. divaricatum* has decreased by 80% and 14% in the gentle and steep slopes over the census years.

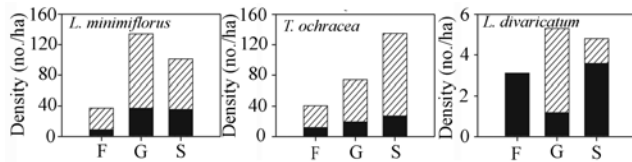


Fig. 2. Mean population density of *L. minimiflorus*, *T. ochracea* and *L. divaricatum* in relation to slope class in Chacocente dry forest. Along the abscissa, F: Flat, G: Gentle slope, and S: Steep slope.

Table 2. Annual rate of change in total density (seedlings, saplings and poles) of *Lonchocarpus minimiflorus*, *Tabebuia ochracea* and *Lysiloma divaricatum* in relation to slope and crown exposition to sunlight classes over a three-year period in Chacocente dry forest.

Slope class	Annualized rate of population change (r)		
	<i>L. minimiflorus</i>	<i>T. ochracea</i>	<i>L. divaricatum</i>
Flat	0.040	0.168	*
Gentle-slope	-0.118	0.066	-0.805
Steep-slope	-0.169	0.031	-0.144
Crown exposure class			
Fully exposed	0.074	0.112	0.00
Partially shaded	-0.212	-0.017	0.091
Overshadowed	-0.020	0.193	*

* ln 0 does not exist

Density in relation to crown exposure to sunlight

The mean population density (averaged over the three census years) of seedlings and saplings of the studied species differed significantly in relation to crown exposure to sunlight ($X^2_{(0.05, 2)} = 136.64$, $p < 0.0001$). Partially exposed individuals of *L. minimiflorus* and *T. ochracea* had the largest density compared with fully exposed and overshadowed individuals (Fig. 3). The density of *L. divaricatum* recruits was generally low irrespective of crown exposure to direct sunlight.

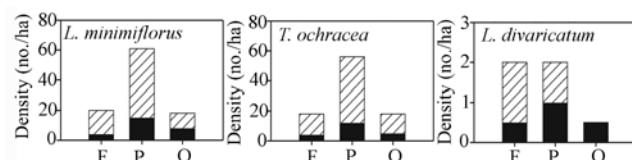


Fig. 3. Mean population density of *L. minimiflorus*, *T. ochracea* and *L. divaricatum* in relation to exposure to sunlight in Chacocente dry forest. Along the abscissa, F: fully exposed, P: partially exposed, and O: overshadowed.

The annualized rate of population change for *L. minimiflorus* showed a 7% increase for fully exposed recruits, but reduced by

21% and 2% for partially exposed and completely overshadowed, respectively (Table 2). While the population of partially exposed recruits of *T. ochracea* decreased by 1.7%, there was an 11% and 19% increases in population of fully exposed and completely overshadowed recruits, respectively. Although the population of fully exposed recruits of *L. divaricatum* remained unchanged, there was a 9% decrease in the population of partially exposed individuals.

Spatial pattern

Analysis of spatial distribution of regenerated individuals indicates that seedling and sapling populations of *L. minimiflorus* and *T. ochracea* displayed a clumped distribution while both seedling and sapling populations of *L. divaricatum* exhibited a uniform pattern (Table 3).

Table 3. Standardized Morisita's Index of the studied species in Chacocente dry forest, Nicaragua over a three-year period (2001–2003).

Species	Size class		
	Seedlings	Saplings	Poles
<i>L. minimiflorus</i>	0.51	0.51	---*
<i>T. ochracea</i>	0.53	0.53	-0.05
<i>L. divaricatum</i>	-0.04	-0.04	---*

* data not available

Discussion

Population dynamics

The results show a striking difference in the density of regenerated individuals among species (Fig. 1). The regeneration of *L. divaricatum* was extremely low compared with the density of *L. minimiflorus* and *T. ochracea*. Establishment, survival and growth of seedlings is governed by several biotic and abiotic factors (Kitajima and Fenner 2000). Arrival of viable seeds to the regeneration sites and subsequent germination and establishment of seedlings are vital determinants of the efficacy of natural regeneration (Felfili 1997). Membreno (2004) reported an average of 413 individuals per hectare for *L. divaricatum* within a radius of 20 m around parent trees in the seedling and sapling classes. In a soil seed bank study carried out in the dry deciduous forest in Chacocente, Uasuf et al. (2009) has found 244 seeds m⁻² for *L. divaricatum*, but none of them was viable. Apparently, the low density of naturally regenerated individuals of *L. divaricatum* could be related to seed dispersal limitation and low seed viability. On the other hand, seeds of *L. minimiflorus* and *T. ochracea* were not encountered in the soil seed bank assessment (Uasuf et al. 2009); indicating that seedling bank could possibly be the recruitment strategy of these two species.

The pattern of natural regeneration of the studied species found in our study agrees with previous studies made in Chacocente and Nandarola (25 km away from Chacocente forest) dry deciduous forests in Nicaragua (Sabogal and Valerio 1998; Cárdenas and Castro 2002). However, the density of naturally

regenerated individuals in our study was comparably lower than that of Sabogal & Valerio (1998). This discrepancy could be related to mortality that might have occurred in the period between the two studies, and the selection of plots for undertaking the study. Unlike their study, our plots represented large environmental variations; particularly slope of the terrain and light conditions.

The annualized rate of change in seedling and sapling densities also varied among species and size classes (Table 1). For instance, the population of *L. minimiflorus* seedling declined by 54% (mainly seedlings that were 10–100 cm in height), while the sapling population slightly increased by 1% from 2001 to 2003. Seedling mortality varies among species, depending on the size and age of seedlings as well as the softness and palatability of tissues (Kitajima and Fenner 2000). Young seedlings are vulnerable to several biotic and abiotic factors (Gerhardt 1998). Predation, herbivory and pathogens are the major biotic factors that affect seedling survival and seedling population densities (Hubbell 1979; Terborgh and Wright 1994; Thomson et al. 1996; Sherman 2002). In addition, periodicity of seed production in some species influences the presence of seedling in a measurement year and their decrease in subsequent assessment (Felfili 1997).

Among the abiotic factors, drought is the chief cause of seedling mortality in tropical dry forests (Gerhardt 1996). Young seedlings are also succumbed to death due to low-intensity ground fires (Saha and Howe 2003) and physical damage induced by litterfall (Clark and Clark 1991; Drake and Pratt 2001), which in turn varies between species (Gillman et al. 2003). Although we did not endeavor to explain the cause of mortality in the present study, the remarkably high seedling mortality in *L. minimiflorus* could be attributed to one or combination of the above factors. However, anthropogenic disturbances, such as cattle grazing and mowing are very common in this forest, and possibly contribute to the decline in population density of the studied species (Sabogal and Valerio 1998; pers. obs.).

The population of *L. divaricatum* slightly increases in the seedling class while saplings suffered an annual reduction of 69%. The estimate of sapling mortality is somehow exaggerated because of the low population density of this species. As a whole, the result indicates that the low population density of this species does not guarantee to maintain its current position in the phytosociological hierarchy of the forest. *T. ochracea* had a positive annual population change from 2001 to 2003 in all size classes. This indicates that regeneration advances well.

Spatial pattern

Regeneration of the studied species varied considerably in relation to slope of the terrain (Fig. 2). For instance, regeneration was relatively high in the gentle slope for *L. minimiflorus* while it was higher in the steep slope for *T. ochracea*. For both species, regeneration was very poor in the flat area, probably due to flooding that might create anaerobic condition thereby preventing germination and seedling growth. However, seedling and sapling mortality was higher in the gentle and steep slope for *L.*

minimiflorus while the population of *T. ochracea* displayed a net positive change irrespective of the slope of the terrain (Table 2). Similarly, regeneration differed substantially among crown exposure to sunlight classes (Fig. 3). Partially shaded seedlings and saplings of *L. minimiflorus* and *T. ochracea* were more abundant than fully exposed ones. This can be further evidenced from spatial analyses (Table 3) where the population of *L. minimiflorus* and *T. Ochracea* displayed a clumped spatial distribution.

Clumped or aggregated spatial pattern is very common among species in tropical forests (Hubbell 1979; Condit et al. 2000). Poor dispersal of propagules and recruitment limitations (soil nutrient, light, moisture, etc) may lead to such pattern (Bun-yavejchwin et al. 2003; Hardy and Sonké 2004). Basnet (1992) and Enoki & Abe (2004) also pointed out that the distribution pattern of trees is affected by numerous biotic and abiotic factors and their interaction, but topography is a major physical factor which affects the composition, growth, and distribution of tropical forest. Other studies also demonstrated topographic habitat association and association with canopy openness (Svenning 1999). The fact that partially shaded recruits of *L. minimiflorus* and *T. ochracea* were relatively abundant compared with fully exposed ones could be one survival strategy to avoid the detrimental effect of damagingly high leaf temperature that can not be ameliorated by cooling through transpiration. Ray and Brown (1995) have shown that medium shade increases survival of Caribbean dry forest species due to its interactive effect with drought tolerance.

In conclusion, the results from the present study provide evidence that natural regeneration alone is not sufficient to restore the population of the studied species in Chacocente, especially for *L. divaricatum* and *L. minimiflorus* for which the populations show a declining trend. Therefore, an immediate measure should be taken to assist the natural regeneration process. Natural regeneration is abundant in slopes than flat terrain and under partial exposure of the crown. Thus, the use of nurse trees in open areas and enrichment planting on the slopes would be useful in future restoration works.

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